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Spatial redistribution of nutrients by large herbivores and dung beetles in a savanna ecosystem

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Abstract

1. Territorial or resting behaviour of large herbivores can cause strong local deposits of dung, in different places than where they graze. Additionally, dung beetles and other macrodetritivores can subsequently affect local nutrient budgets through post-depositional re-dispersion of dung and accompanying nutrients. Such horizontal displacement of nutrients by animals has strong implications for savanna ecosystem functioning, but remains poorly studied as it is notoriously difficult to accurately map these flows and incredibly time-consuming.
2. In an African savanna, with alternating patches of lawn, bunch grasses and trees/shrubs, we undertook such effort and studied nutrient aggregation and redistribution by different large herbivore functional groups and dung beetles for a full growing season. We used movable cages to quantify herbivore consumption rates and measured nutrient return through biweekly dung counts. Furthermore, we estimated the offtake of nitrogen (N) and phosphorus (P) by the dominant megagrazer (white rhinoceros) to middens (dung deposition hotspots). Last, we experimentally measured the removal amount and movement paths of telocoprid dung beetles to quantify their nutrient redistribution effects.
3. Our estimates suggest white rhinoceros to cause a large export of nutrients from grazing areas towards middens resulting in negative nutrient budgets for both lawn and bunch grassland types. Mesograzers (50–600 kg) realized a net nitrogen input towards high forage quality lawn vegetation at the expense of lower quality bunch grasslands. Browsers caused a net flow from trees/shrubs towards grassland patches.
4. Interestingly, while the magnitude of our estimated flows of N consumption and return by large herbivores were rather similar, the P returns were about half of what has been consumed. This is in agreement with ecological stoichiometry theory that predicts that large herbivores should recycle more N than P, due to their relatively high P demand. Furthermore, dung-rolling beetles had a small, but significant, directed movement from lawn to bunch grassland vegetation.
5. *Synthesis*. We conclude that within-ecosystem nutrient redistributions by animals are important and approximately of the same order of magnitude as regional atmospheric nutrient in and outputs (e.g. fire emissions, atmospheric N deposition, biological N fixation), and hence are important for understanding savanna ecosystem functioning.

KEYWORDS
consumer-driven nutrient cycling, ecological stoichiometry, Hluhluwe–iMfolozi Park, megaherbivore, nitrogen, nutrient aggregation, phosphorus, white rhinoceros

1 | INTRODUCTION

The spatial redistribution of nutrients by large herbivores has been identified as an important potential mechanism to increase the spatial heterogeneity in plant nutrient availability in terrestrial ecosystems (Augustine & Frank, 2001; Steinauer & Collins, 1995). The most important direct effects of large herbivores likely follow from local removal of nutrients through ingestion of plant material across the landscape and concentrating it at specific locations by dung and urine deposition, thereby locally strongly increasing nutrient availability (Augustine & Frank, 2001; Steinauer & Collins, 1995; Wolf, Doughty, & Malhi, 2013). The potential magnitude of this effect is best exemplified by the highly increased levels of soil nutrients in corrals or bomas, as a result of overnight containment of livestock to protect against predation (Augustine, 2003; Fox, Bonnet, Cromsigt, Fritz, & Shrader, 2015; van der Waal et al., 2011; Veblen, 2012). However, few studies have quantified both nutrient offtake (ingestion) and return (faecal deposition) by large herbivores in natural ecosystems that are both needed to determine the magnitude of spatial redistribution of nutrients (but see Augustine, McNaughton, & Frank, 2003; Frank & McNaughton, 1992). This calls for a structured approach in which local nutrient balances are quantified that can subsequently be used to estimate the different types of nutrient aggregation and dispersion.

African savannas are well-known for their high biomass of large mammalian herbivores that exert strong effects on ecosystem functioning (Scholes & Archer, 1997). So far, three lateral flows of nutrients by large herbivores in African savannas have gained some support (Figure 1). First, browsing herbivores deposit dung and urine also in open areas and hence transport nutrients from woodland to grassland sites (Sitters, Edwards, Suter, & Venterink, 2015). Second, grazing herbivores cause a net N input in nutrient-rich and net N loss from nutrient-poor sites, due to the different amounts of time spent in each habitat type, increasing spatial heterogeneity in soil and plant nutrients across the landscape (Augustine et al., 2003). Furthermore, shady conditions beneath canopy of woody species can be preferentially used by grazing herbivores as a resting place during the hottest time of the day, that concurrently produce faeces, which can result in a net nutrient flow from grasslands to woody patches (Dean, Milton, & Jeltsch, 1999; Treydte, Riginos, & Jeltsch, 2010). We here extend this emerging framework with two additional nutrient flows that we hypothesize to be important in understanding spatial dynamics of nutrients in African savannas.

First, the two extant pure-grass consuming megagrazers, white rhinoceros (*Ceratotherium simum*) and hippopotamus (*Hippopotamus amphibius*), are both known to feed in quite different areas than where they defecate. Due to their large body size, both species are insensitive to predation and can afford to have strong daily routines, always

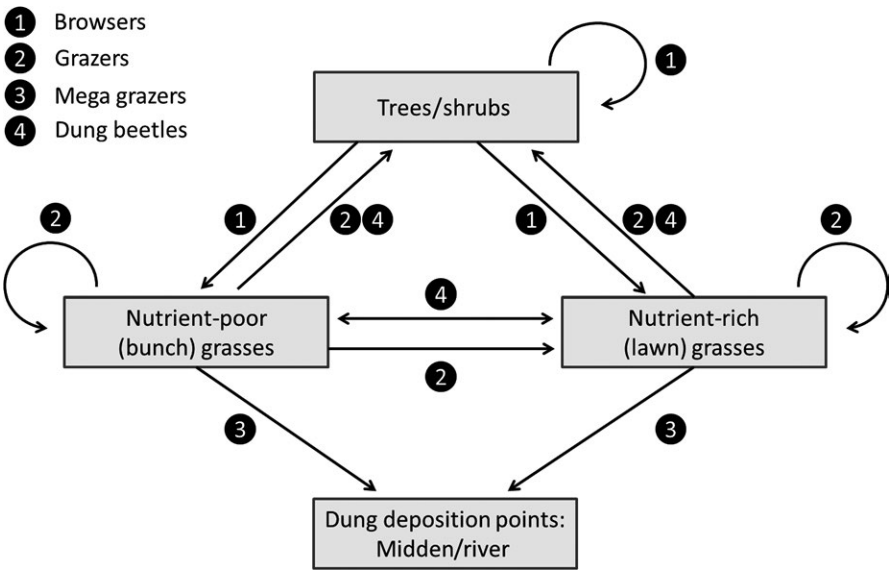

FIGURE 1 Overview of the hypothesized horizontal nutrient flows between vegetation types and dung deposition points for four different functional groups of animals. (1) Browsing herbivores consume nutrients from woody species and deposit urine and dung below trees or redistribute them to grasslands. (2) Grazers consume nutrients from grasses to redistribute them below woody species or within the grass layer through dung and urine deposition. Within grasslands, they have been shown to redistribute nutrients from nutrient-poor areas towards nutrient-rich areas. (3) Megagrazers, such as white rhinoceros and hippopotamus, consume grasses and are known to deposit their dung at specific deposition points (middens, rivers). (4) Dung beetles can redistribute dung after herbivores deposited the dung, possibly resulting in flows between the vegetation types

grazing and defecating in the same place, without the risk of being stalked by a predator upon the next return. Hippos make daily feeding migrations between more upland savanna grasslands where they forage and aquatic systems (rivers, wetlands and lakes) where they rest (Kanga, Ogutu, Piepho, & Olff, 2013). It is estimated that half of their excretion/egestion enters these aquatic ecosystems, causing major redistribution of nutrients from terrestrial into aquatic systems (Subalusky, Dutton, Rosi-Marshall, & Post, 2015). White rhinos defecate in middens, where the associated scent marking is a key part of their territorial behaviour (Owen-Smith, 1971). As far as we know, the importance of nutrient export into middens by white rhinoceroses has not yet been quantified. Nevertheless, scaling law-derived estimates show that larger animals play a disproportionate large role in the horizontal transfer of nutrients across the landscape (Doughty, Wolf, & Malhi, 2013; Wolf et al., 2013), suggesting an important role of megagrazers in this. This provides megaherbivores with a unique potential role in creating and maintaining landscape heterogeneity by nutrient aggregation.

Second, macrodetritivores as termites and dung beetles may play an important role as such redistributors of nutrients, in addition to their key role in dung decomposition and hence nutrient mineralization (Freymann, Buitenwerf, Desouza, & Olff, 2008; Veldhuis, Laso, Olff, & Berg, 2017). Moreover, the clades of telocoprid dung beetles redistribute freshly produced dung of large herbivores between vegetation types (Davis, 1996) and could therefore have an important effect on nutrient heterogeneity and cycling. Although previous work suggests that dung beetles (Davis, 1996; Nichols et al., 2008) and termites (Freymann et al., 2008) can remove large amounts of dung in short amounts of time, the magnitude and direction of this post-depositional dung dispersal remains unclear.

Here, we investigated the amounts of nutrients ingested by grazers from the grass layer in a vegetation mosaic (of lawn and bunch grass types) for a full growing season using movable large herbivore exclusion cages. We quantified the nutrient deposition by large herbivores through biweekly dung counts at the same sites and estimated N and P return from dung to urine deposition using literature-based conversion values. We estimated the translocation of N and P by the dominant megagrazer (white rhinoceros) by calculating the deviations from power-law scaling relationships between dung counts and metabolic biomass densities of large herbivores. Last, we performed a dung removal experiment in which we quantified the amount of nutrients translocated by telocoprid dung beetles and tracked the movement of those beetles and their dung balls to determine burial location to investigate the occurrence of directional displacement of dung. When put together, with these measurements, we were able to estimate the main pathways through which browsers, mesograzers, white rhino and dung beetles redistribute nutrients in this savanna ecosystem, as outlined in Figure 1.

2 | MATERIALS AND METHODS

This study was performed in Hluhluwe–iMfolozi Park (HiP), a 900-km^2 game reserve in Kwa-Zulu Natal, South Africa. Vegetation structural types range from open grasslands to closed *Acacia* and broad-leaved woodlands (Whateley & Porter, 1983). The grassy vegetation is characterized by a high heterogeneity with short grazing lawns ranging in size between a few square metres to a couple of hectares that alternate with tall grasslands dominated by bunch/tussock-forming species. We selected five sites with relatively similar annual rainfall (532–663 mm/year), similar soil texture (median particle size of 0.05–0.15 mm) and woody cover (ranging from 16% to 37%) (see Table S1 in Appendix S1). At each site, we measured nutrient ingestion and dung deposition by large herbivores and dung displacement between vegetation types via a dung removal experiment.

2.1 | Nutrient ingestion

Nutrient ingesting through grazing by large herbivores was quantified using movable cages (McNaughton, Milchunas, & Frank, 1996). On each site, we established three iron cages of 1 × 1 × 1 m on both lawn and bunch grass areas. Cages were moved every 20 to 42 days for one full growing season between September 2013 and May 2014. All grass within the cages was clipped before moving to a new plot, after which their mass was measured and compared with the mass in the control plots next to the cages. For more detailed information about the methods regarding movable cages, see Veldhuis, Fakkert, Berg, and Olff (2016). All clipped biomass samples were labelled and taken back to the laboratory where they were dried (48 hr at 70°C), weighed, ground (Foss Cyclotec, 2 mm mesh size), stored in small plastic pill bottles and shipped to the University of Groningen. Leaf N (%) content was estimated using a Bruker near-infrared spectrophotometer (NIR, Ettlingen) using a multivariate calibration of foliar samples measured both on the NIR and CHNS EA1110 elemental analyser (Carlo-Erba Instruments, Milan). Cross-validation showed the NIR spectra predicted N content highly accurate (R^2 = 0.96, N = 1,759). To determine leaf phosphorus content, 0.5 g ground leaf sample was destructed with 8 ml 65% HNO_3 in a Teflon-lined glass tube by pressurized microwave digestion using a CEM discover SPD (CEM Corporation, NC, USA). Subsequently, P contents were measured using a continuous flow-analyser (Technicon AutoAnalyzer II), with molybdenum and vitamin C colorization at 820 nm. The amount of grass consumed by herbivores multiplied by their N and P contents were used as estimates for nutrient ingestion by large herbivores for each time period (mg m^{-1} day^{-1}).

2.2 | Nutrient deposition by large herbivores

A permanent grid (50 m × 25 m) was set up at each of the five sites consisting of 50 squares of 5 by 5 m. Subsequently, every 2 weeks a dung count was performed within these grids. The amount of dung pellets/piles, herbivore species and the vegetation type (lawn grass, bunch grass or woody vegetation) on which the dung was dropped were determined for each square. When a dung pile was counted, we broke the pellet/pile to avoid repetition 2 weeks later in such a way that it could neither be confused with animal trampling nor

environmental effects like rainfall. Dung counts were carefully undertaken with two persons to reduce the possibility of missing piles to a minimum. If in the improbable case dung piles have been missed, these most likely represent the smaller herbivore species as these are less notable. It therefore also represents a small amount of dung and thus would be implausible to have a substantial effect on our analyses. Subsequently, to estimate deposited N and P from our dung count data, we established a database of pellet/pile dry weight, %N, %P, urine N:dung N ratio, grazer and browser index for every herbivore species, based on a literature survey (Table S2 in Appendix S1). Hippopotamus was not included in this study as we did not encounter a single dung pile at our sites during this study; their abundance is very low in HiP. Average body masses for all species were taken from Smith et al. (2003). Dry weight of individual dung pellets for African elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*) and warthog (*Phacochoerus africanus*) were obtained from Sitters, Maechler, Edwards, Suter, and Venterink (2014). Greater kudu (*Tragelaphus strepsiceros*) dung pellets were assumed to weigh similar to giraffe. Dung pile dry weights were obtained for African buffalo (*Syncerus caffer*) from Sitters et al. (2014), and for grey duiker (*Sylvicapra grimmia*), impala (*Aepyceros melampus*) and blue wildebeest (*Connochaetes taurinus*) from van der Waal et al. (2011). Nyala (*Tragelaphus angasii*) dung pile weight was assumed to be similar to impala dung pile weight. White rhinoceros (*Ceratotherium simum*) dung pellet and complete pile dry weight were determined in the field during this study.

African buffalo, warthog, blue wildebeest, white rhinoceros and Burchell's zebra were treated as obligate grazers, while grey duiker, giraffe and greater kudu assumed to be obligate browsers (Codron & Codron, 2009). African elephant was seen as mixed feeder (Codron et al., 2011). Impala was considered a grazer and nyala, a mixed feeder based on stable isotope analyses of faeces in the same park that showed over 80% C4 grass signal for impala during the wet season and *c.* 60% for nyala (Botha & Stock, 2005).

The N and P content of dung for African buffalo, African elephant, grey duiker, giraffe, warthog, blue wildebeest and Burchell's zebra were taken from Sitters et al. (2014). The N content of dung from impala, greater kudu and nyala were obtained from Codron et al. (2007). The P content of impala and greater kudu dung was acquired from Wrench, Meissner, Grant, and Casey (1996) and for nyala we took the mean %P of the other species. For white rhinoceros, the N and P contents were determined through chemical analysis similar to the methods used for grasses described above.

Urine deposition was calculated from dung deposition rates (Augustine et al., 2003; Frank, Inouye, Huntly, Minshall, & Anderson, 1994). We used the same values for urine N:dung N ratios as Sitters et al. (2015) for African buffalo, grey duiker, giraffe, greater kudu, nyala, warthog and blue wildebeest. For impala and zebra, we used values obtained from Augustine et al. (2003) for urine N:dung N ratios and for African elephant and white rhinoceros, we averaged the ratios of the other species. Furthermore, we corrected the N return via urine deposition by 25% to account for ammonia volatilization (Ruess & McNaughton, 1988).

2.3 | Robustness of nutrient deposition estimates

Our estimates of nutrient deposition (and redistributions) depend on values extracted from literature. For some species no data were available, so that mean values of other species have been used as a best possible estimate. Also, when data were available, these were often measured in different game reserves. To test the robustness of our estimates (and final conclusions), we therefore not only quantified the best possible estimates but also estimated the nutrient deposition and redistributions based on the minimum and maximum values across species (Table S2 in Appendix S1).

2.4 | Nutrient translocation by white rhinoceros from grazing areas to middens

We used power-law scaling functions, commonly used to scale biological variables to body size (Brown, Gillooly, Allen, Savage, & West, 2004; Kleiber, 1932; West, Brown, & Enquist, 1997), to model relationships between total dung deposition per day at the five sites (g ha^{-1} day^{-1}) and average metabolic biomass densities ($kg^{0.75}$ ha^{-1}) for the park per species. Body mass for each herbivore species were obtained from Smith et al. (2003) and herbivore densities from Ezemvelo KZN Wildlife (Census data 2014, unpublished). We constructed 90th quantile linear regression models to describe the general pattern between metabolic biomass density and (maximum) dung production for all herbivores. Subsequently, model residuals were investigated to identify species that deviated from the general pattern (lower dung production than expected based on metabolic biomass density) between metabolic biomass density and dung production (Table 1). Generally, browsers showed higher deviations than grazers, probably because they use a slightly different habitat, which is exemplified by the high residuals of nyala that is generally found in dense habitats. White rhinoceros was the only grazer experiencing remarkably high residuals. We attributed this to the specific defecating behaviour of white rhinoceros, depositing dung in their middens, resulting in decreased dung production inside our plots. Consequently, we used the difference between the actual amount of white rhinoceros dung found in our plots and expected dung based on the constructed power-law scaling functions (residuals ± *SE* (obtained by bootstrapping)) to estimate the percentage of dung exported by white rhinoceros.

2.5 | Nutrient translocation by telocoprid dung beetles

To determine how many nutrients were translocated by ball-rolling dung beetles and whether they exhibit directional movement across vegetation types, we performed a dung removal experiment. We used white rhinoceros dung as this was the species of interest in the study, and fresh dung was abundantly available. Fresh dung was collected from middens at the side of the road in early mornings and two 8–10 kg (average white rhinoceros dung pile) dung heaps were then placed at one of our five sites. We chose very heterogeneous sites in terms of vegetation so that distinct vegetation types alternate across several metres

TABLE 1 List of common herbivores in Hluhluwe–iMfolozi Park, South Africa. For each species, the functional group, body mass, metabolic biomass, daily dung production and residuals from 90th quantile linear regression power-scaling functions between dung produced and metabolic biomass density (Figure 3) are given. Herbivore densities are not presented, whereas densities of white rhinoceros are conservation-sensitive information

Species	Scientific name	Functional groups	Body mass (kg)	Metabolic biomass ($kg^{0.75}$)	Dung produced ($g\ ha^{-1}\ day^{-1}$)	Residuals
Buffalo	*Syncerus caffer*	Grazer	580	118.2	1,017.5	0.00
Elephant	*Loxodonta africana*	Mixed	3,940	497.3	432.7	−0.10
Giraffe	*Sylvicapra grimmia*	Browser	900	164.3	23.0	−1.35
Grey duiker	*Giraffa camelopardalis*	Browser	19.5	9.3	1.3	−1.81
Impala	*Aepyceros melampus*	Grazer	52.5	19.5	199.9	−0.42
Kudu	*Tragelaphus strepsiceros*	Browser	213.5	55.9	9.1	−1.41
Nyala	*Tragelaphus angasii*	Mixed	86.6	28.4	8.6	−2.69
Warthog	*Phacochoerus africanus*	Grazer	82.5	27.4	46.5	−0.84
White rhino	*Ceratotherium simum*	Grazer	2,950	400.3	124.2	−2.36
Wildebeast	*Connochaetes taurinus*	Grazer	180	49.1	52.5	0.00
Zebra	*Equus burchellii*	Grazer	276	67.7	76.6	−0.49

and therefore all vegetation types were always in close proximity and within reach of dung beetle movement to create a choice experiment for beetles. About 10 g of fresh dung was taken to determine fresh to dry weight ratio (70°C, 48 hr). One dung pile was placed straight on the underlying vegetation, and the second pile was placed on a metal mesh (1 m diameter, 1.4 mm mesh size) that was secured to the ground to exclude the transport of dung down the soil profile by tunnelling dung beetles. Furthermore, a small control bag (10 × 3 cm, mesh = 1.4 mm) with 10 g of the same dung was placed inside each dung pile to determine dung loss by microbial decomposition. After 4 days, the dung piles and control bags were collected and dried (70°C, till dry). Using the fresh to dry weight ratios, mass loss of the dung pile was estimated. Dung mass loss of control bags after 4 days was attributed to microbial decomposition and corrected for in subsequent analyses. In total, this experiment was replicated 14 times, equivalent to a total of 28 dung piles (between 2 December 2013 and 8 February 2014).

After dung piles were placed, telocoprid dung beetles almost immediately colonized the dung and started forming dung balls. We followed different species of individual dung beetles rolling their ball away from the dung pile to a burial location. All followed dung beetles belonged to one of the three most dominant telocoprid dung beetle species: *Kheper nigroaeneus* (n = 13), *Allogymnopleurus chloris* (n = 20) and *Gymnopleurus humanus* (n = 18) (all Coleoptera; Scarabaeidae). We placed small coloured wooden sticks along their path every minute without disturbing the beetles, identifying the movement path. When the dung beetle had buried its dung ball, the absolute distance (to the nearest cm) to the dung pile was measured with a tape measure and vegetation around every wooden stick was recorded (including burial place). Across the five sites, a total of 51 dung beetles were followed and observed percentages of dung balls buried in each vegetation type (lawn grass, bunch grass or woody vegetation) were calculated for each site. To determine whether dung beetles randomly buried their dung balls or selected for a specific vegetation type, we calculated expected ("no selection") percentages vegetation type in three different ways. First, we used the percentages of vegetation types around the wooden sticks for each dung beetle as an expected value, representing the distribution of vegetation types that each individual dung beetle encountered. Second, we mapped all three vegetation types every metre (up to 15 m) from each dung pile along linear transects from the starting point in the eight main compass directions (N, NE, E, etc.) and calculated the percentage of each vegetation type at the distance of burial (n = 8) for each individual dung beetle. This would represent the expected values when dung beetles would have an optimal burial distance (Connell, 1971; Janzen, 1970). Third, we calculated the percentage of each vegetation type within this total area of the 15 m radius (n = 120) and used that as a third expected distribution. This way, our three expected values represented different assumptions on dung beetles decision-making (i.e. encounters, optimal distance, random) and we could test preferences for a specific vegetation type based on each assumption to investigate whether they exhibit directional movement.

2.6 | Data analysis

Basic statistical tests used included paired t tests and Pearson chi-squared tests. Power-law scaling functions were modelled using quantile regression within the "quantreg" package in R (Koenker, 2015), with log-transformations of both dung deposition and metabolic biomass densities. All statistical analyses were executed in R 3.2.2 (R Core Team, 2016).

3 | RESULTS

3.1 | Nutrient ingestion

On average, large herbivores ingested somewhat more N from bunch grassland (21.3 ± 2.6 mg $m^{-2}\ day^{-1}$) than from lawn grasslands

(17.7 ± 7.3 mg m^{-2} day^{-1}) over our 224-day study period, but this was not significantly different (Figure 2; paired *t* test: $t = 1.51$, $df = 4$, $p = .21$). Similarly, somewhat more P was ingested by large herbivores from bunch grasslands (2.57 ± 0.56 mg m^{-2} day^{-1}) than lawn grasslands (2.06 ± 0.93 mg m^{-2} day^{-1}), but this was also not significantly different (Figure 2; paired *t* test: $t = 1.13$, $df = 4$, $p = .32$).

3.2 | Nutrient deposition by large herbivores

Large herbivores deposited more N (paired *t* test: $t = 3.02$, $df = 4$, $p < .05$) and P (paired *t* test: $t = 5.02$, $df = 4$, $p < .01$) per unit area lawn grassland than bunch grassland (Table 2, Figure 2). These differences were caused by grazing herbivores that deposited significantly more nutrients on lawn than bunch grasslands (paired *t* test: N: $t = 4.87$, $df = 4$, $p < .01$; P: $t = 5.40$, $df = 4$, $p < .01$), whereas browsers showed no preferences (paired *t* test: N: $t = 0.58$, $df = 4$, $p = .58$; P: $t = 0.43$, $df = 4$, $p = .68$).

Subtracting the amount of nutrients deposited from the amount ingested resulted in net nutrient losses for both vegetation types (Figure 2). On average, bunch grasslands lost *c.* 57% of the N consumed by large herbivores (12.1 mg m^{-2} day^{-1}), whereas lawn grasslands were depleted significantly less by about 33% (5.7 mg m^{-2} day^{-1}, paired *t* test: $t = -3.17$, $df = 4$, $p < .05$). The percentage lost P was overall substantially higher than N loss, where bunch grasslands lost *c.* 79% of consumed P (2.04 mg m^{-2} day^{-1}) and lawn grasslands *c.* 66% on average (1.36 mg m^{-2} day^{-1}), but this was not significantly different between vegetation types (paired *t* test: $t = -1.55$, $df = 4$, $p = .20$).

Furthermore, our estimates suggest that grazers translocated about the same amount of nutrients to woody patches as browsers towards grasslands for both N (Table 2; paired *t* test; lawn: $t = 1.04$, $df = 4$, $p = .35$; bunch: $t = 1.39$, $df = 4$, $p = .23$) and P (paired *t* test; lawn: $t = 1.17$, $df = 4$, $p = .31$; bunch: $t = 1.84$, $df = 4$, $p = .14$).

3.3 | Nutrient translocation by white rhinoceros

There was a clear relationship between metabolic biomass densities of herbivores and dung deposition at our sites (Figure 3). The 90th quantile linear regression identifies the maximum dung deposition expected at our sites for each herbivore species. Deviations from this regression (lower dung production than expected) were investigated by calculating residuals (Table 1). Grazers generally showed low residuals (0–0.84), whereas deviations of observed dung deposited by browsers were larger (1.35–2.69). White rhinoceros was the largest exception from these general trends, with exceptionally low dung deposition for a grazing herbivore. This deviation of white rhinoceros from the general trend was attributed to its specific defecation behaviour (highly predictable dung deposition in middens) and used to estimate the magnitude of export flow. Comparison of observed dung counts and expectations following our regression, 91.3% (*SE*: 83.9%–94.5%) of dung is exported by white rhinoceros, which is equivalent to 7.3 mg N m^{-2} day^{-1} and 0.40 mg P m^{-2} day^{-1} from bunch grasslands and 9.2 mg N m^{-2} day^{-1} and 0.51 mg P m^{-2} day^{-1} from lawn grasslands (Figure 2). This asymmetry in estimated nutrient export by white rhinoceros from lawn to bunch grasslands results from using actual dung deposited in each vegetation type (*c.* 26% more in lawn grasslands) as an indicator of nutrient ingestion. This is based on the assumption that they will produce relatively more dung in the vegetation type where they forage most.

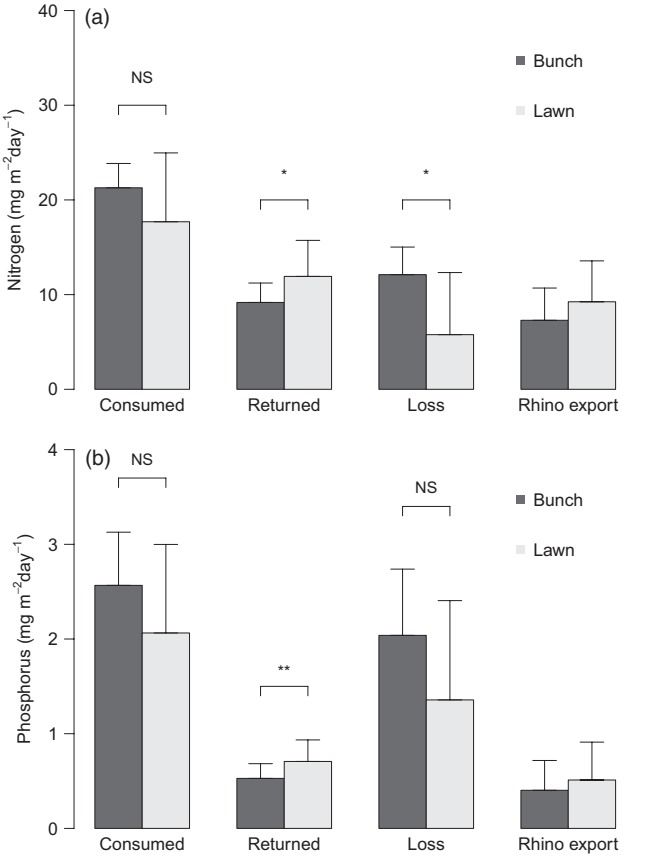

FIGURE 2 Amounts of nitrogen (a) and phosphorus (b) consumed and returned by large herbivores, overall loss of nutrients and estimated export by white rhinoceros for lawn and bunch grasslands. Significance levels: NS > 0.1, * < .05, ** < .01

3.4 | Nutrient translocation by dung beetles

On average, 26.3% of the dry weight of each experimental dung pile was translocated by dung beetles within 4 days. No other major actors of dung translocation than dung beetles were observed in this initial period. Variation between dung piles was large, ranging from 1% to 61% dung removal. Microbial decomposition over this time interval was negligible and only accounted for *c.* 2% of dung mass loss. Furthermore, dung piles without mesh covering the soil experienced higher dung removal percentages (30.9%) than dung piles with mesh (21.7%) (paired *t* test: $t = 2.02$, $df = 13$, $p < .05$), suggesting that rolling dung beetles removed *c.* 20% and ground-tunnelling beetles removed *c.* 9% of the initial dung pile (after correction of microbial decomposition).

	N deposition			P deposition		
	Grazers	Browsers	Total	Grazers	Browsers	Total
Lawn	10.0 (3.2)	2.0 (1.9)	12.0 (3.8)	0.65 (0.24)	0.06 (0.06)	0.71 (0.23)
Bunch	7.5 (2.4)	1.7 (1.1)	9.2 (2.0)	0.48 (0.18)	0.05 (0.03)	0.53 (0.15)
Tree/shrub	1.2 (0.6)	0.4 (0.5)	1.7 (0.9)	0.09 (0.05)	0.01 (0.01)	0.10 (0.04)

TABLE 2 The average amounts of nitrogen (N) and phosphorus (P: mg m^{-2} day^{-1}, with *SD*) deposited in urine and dung combined for three different vegetation types at our five sites, for grazers, browsers and all herbivores together respectively

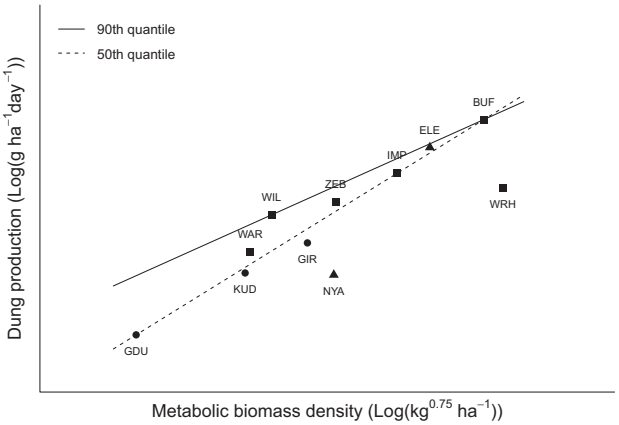

FIGURE 3 Total dung production at our five sites as a function of metabolic biomass densities of the 11 most common herbivores in Hluhluwe–iMfolozi Park. Both axes are log-transformed. Axis values are not presented, whereas densities of white rhinoceros represent conservation-sensitive information. Regression lines represent 50th and 90th linear quantiles

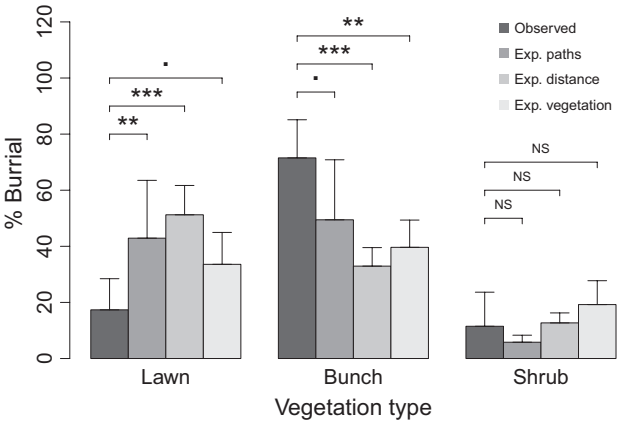

FIGURE 4 Observed and expected percentage of times dung beetles buried their dung balls within each vegetation type. Error bars indicated *SD*s. Significance levels: NS > 0.1, ■ < .1, ** < .01, *** < .001

We followed 42 dung beetles to determine their burial locations, of which 17% buried their ball in lawn grasslands, 72% in bunch grasslands and 11% under cover of woody species. Dung beetles buried their balls less often than expected in lawn grasslands (comparing expectations based on availability with actual use, Figure 4), either when expectations were based on the encountered vegetation types along their rolling paths ($\chi^2 = 6.7$, $p < .01$) or as encountered at a predetermined burial distance ($\chi^2 = 11.4$, $p < .001$), but not when compared to the % lawn cover in the area in general, although nearly significant ($\chi^2 = 3.2$, $p = .07$). In contrast, burial of dung balls was higher than expected for bunch grasslands, both based on optimal distance ($\chi^2 = 11.9$, $p < .001$) and overall % bunch grass ($\chi^2 = 6.8$, $p < .01$), but not when compared to encounters during their walk, although nearly significant ($\chi^2 = 3.7$, $p = .054$). The percentage of dung balls buried under shrubs or trees did not differ significantly from expected values (along paths: $\chi^2 = 0.3$, $p = .60$; predetermined distance: $\chi^2 = 0.001$, $p = .96$; overall vegetation: $\chi^2 = 1.2$, $p = .27$).

3.5 | Overview horizontal spatial nutrient flows

Combining all the acquired information we were able to quantify the proposed flows in Figure 1 in an overview of horizontal spatial nutrient fluxes by the interplay by large herbivores and dung beetles (Figure 5), where the numbers in the subsequent text referring to the arrows in this figure.

1. First, we measured nutrient depositions by browsers in woody patches, as well as in lawn and bunch grasslands (Table 2) and converted these into horizontal nutrient flows.
2. Second, we measured nutrient deposition rates by grazers in woody patches, lawn and bunch grasslands (Table 2) and converted these to horizontal nutrient flows making the following assumptions. Our study design and methods did not allow us to distinguish whether the nutrients deposited by grazers originated from lawn or bunch grasslands. We therefore assumed that flows from lawn to bunch grasslands towards woody patches were equal as this was the least subjective choice. Note that the magnitudes of these flows are relatively small and other assumptions would not have changed the overall conclusions of this study. Furthermore, as nutrient deposition by grazers was higher in lawn than bunch grasslands, and nutrient ingestion did not significantly differ between the two grass vegetational types (Figure 2), the overall result is a net nutrient flow from bunch to lawn grasslands. The estimated nutrient flow from bunch to lawn grasslands ranges from 1.2 mg N m^{-2} day^{-1} and 0.09 mg P m^{-2} day^{-1} (assuming most nutrients deposited on lawn grassland also originated from lawn grasslands) to 8.7 mg N m^{-2} day^{-1} and 0.57 mg P m^{-2} day^{-1} (assuming all deposited nutrients on lawn grasslands originated from bunch grasslands). We chose to present the net flow and therefore the most conservative estimates in Figure 5.
3. Third, we estimated the amount of nutrient translocated by white rhinoceros towards dung deposition points, based on deviations

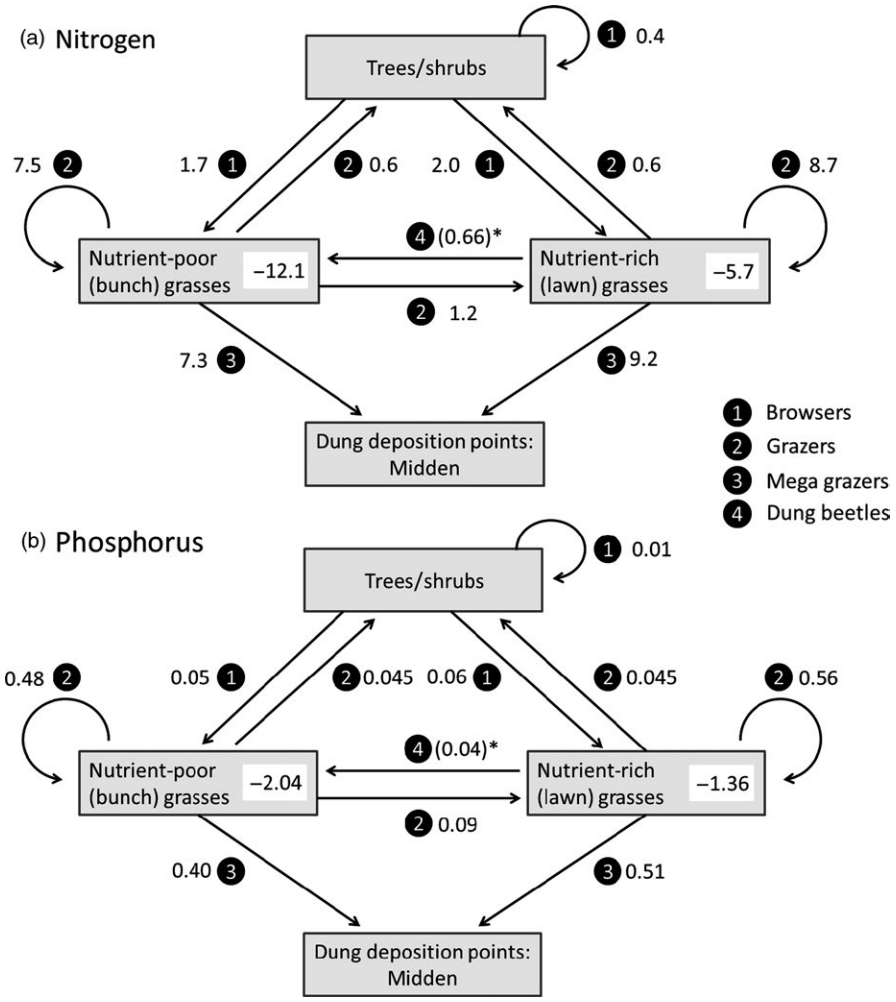

FIGURE 5 Overview of estimates of horizontal flows of nitrogen (a) and phosphorus (b) between different vegetation types and dung deposition points for four functional groups of animals. Values represent mg m^{-2} day^{-1} over a 224-day study period (full growing season). Values inside the white boxes represent overall balances per vegetation type as determined by the local difference between nutrients ingested (measured through movable cages) and returned (measured through dung counts). *These estimates of nutrients redistributed by dung beetles follow from generalizations from our experiment and validity of this generalization is highly uncertain. Numbers are merely presented to obtain an idea of the possible impact

from relationships between dung deposition and metabolic biomass densities of 11 common herbivores.

4. Finally, we quantified percentage dung translocated by telocoprid dung beetles (*c.* 20%) and showed they exhibit directional movement from lawn to bunch grasslands (*c.* 28%). Together this yields an estimate of 5.6% of post-depositional dung dispersal by dung beetles from lawn to bunch grasses.

3.6 | Robustness of redistribution estimates

Using minimum dung nutrient concentrations and urine N:dung N ratios instead of species-specific concentrations and ratios decreased the overall estimates of N deposition by grazers with *c.* 20%, while for browsers this N deposition was reduced with about 40% (Table S3 in Appendix S1). For P, this pattern was reversed, with reductions of about 50% for grazers and less than 20% for browsers. Overall, N flows were reduce by about 20% and P flows by about 45% when using these minimum instead of species-specific estimates. When using maximum dung nutrient concentrations and urine N:dung N ratios, N flows were increased by *c.* 180% for grazers and *c.* 90% for browsers, when compared to species-specific estimates. Estimates of P flows almost doubled for grazers when using maximum estimates, while for browsers these estimates almost tripled.

Estimated flows for export of nutrients by white rhinoceros almost decreased by 50% under the assumption that 83.9% instead of 90.6% of the white rhinoceros faeces were exported to middens, and almost doubled assuming 94.5% was removed. These percentages represent the mean (90.6%) and the *SE*s (83.9% and 94.5%) of the residuals following the quantile regression of herbivore metabolic biomass densities and dung production (Figure 3).

These minimum (Figure S1 in Appendix S1) and maximum estimates (Figure S2 in Appendix S1) for nutrient deposition, redistribution and export can then be summarized (similar to Figure 5) and their accuracy can be investigated by comparing estimates of nutrients removed from lawn to bunch grasslands based on the flow estimates (arrows departing from the boxes) with the amount of N and P consumed from each vegetation type (based on the movable cages). Theoretically, the amount of nutrients redistributed cannot exceed the amount of nutrients ingested (their ratio should be <1). Ratios between estimated N redistributed and N consumed exceed this threshold by far for our maximum estimates (Table S4 in Appendix S1; lawn: 2.43, bunch: 1.80) are close to 1 for species-specific estimates (lawn: 1.04, bunch: 0.78) and fall below 0.75 for minimum estimates (lawn:

0.72, bunch: 0.55). For P, these ratio are close to 1 for maximum estimates (Table S4 in Appendix S1; lawn: 1.02, bunch: 0.69), about half for species specific estimates (lawn: 0.54, bunch: 0.39) and below 0.3 for minimum estimates (lawn: 0.28, bunch: 0.19). Overall, this suggests that our maximum estimates of nutrient redistributions are excessively high and not very realistic. Following our minimum estimates, large amounts of nutrients are metabolized by herbivores (or lost into an unknown sink) and therefore could be viewed as very conservative estimates of nutrient redistributions. Our species-specific estimates seem to be most accurate, although there is more P than N metabolized by herbivores.

4 | DISCUSSION

The main objective of this study was to quantify the nutrient ingestion, deposition and translocation in this savanna landscape and how this depends on herbivore size and functional group (grazers vs. browsers). We estimated that white rhinoceros (megagrazer) had a very large effect translocating nutrients to deposition points, i.e. middens, overriding all other horizontal nutrient flows, resulting in large negative nutrient balances for grasslands. In contrast, dung beetles showed smaller effects, but nevertheless caused a net flow from lawn to bunch grasslands. Also, our study suggests that mesograzers enriched nutrient-rich lawn grasslands at the expense of nutrient-poor bunch grasslands. Furthermore, while our best estimates of N ingestion and deposition (including translocation by white rhinoceros) were comparable, we found a gap in the P budgets with almost 40%–60% of the P ingested not being deposited to the ecosystem as dung or urine (accounting for translocation by white rhinoceros), which we discuss below in more detail. Last, although our analyses using minimum and maximum values did result in quantitative changes in our estimates on horizontal nutrient distributions, they did not alter our results qualitatively, neither affect the final conclusions. We therefore continue the discussion using the results from our analyses using species specific estimates.

Previous studies on megaherbivores have positioned them as drivers of ecosystem structure and functioning, exhibiting disproportionately large effects compared to smaller herbivores (Owen-Smith, 1988; Waldram, Bond, & Stock, 2008). Recently, Cromsigt and te Beest (2014) showed empirically that the megagrazer white rhinoceros increased vegetation heterogeneity in Kruger National Park. Our study provides evidence that white rhinoceros also increase heterogeneity of nutrient availability across the landscape. Subalusky et al. (2015) already discussed the important effect of another megagrazer, hippopotamus, on horizontal nutrient flows, which together with our study clearly demonstrates the large impact of megagrazers on nutrient cycling within African savanna ecosystems. However, an important difference between the two megagrazers is that hippopotamus translocates nutrients towards aquatic ecosystems, effectively more permanently exporting nutrients from the terrestrial ecosystem. Only in downstream floodplains, these nutrients may return to terrestrial ecosystems again. In contrast, white rhinoceroses concentrate nutrients at specific points within the landscape (middens).

Our results suggest that mesograzers were responsible for a net flow of N and P from nutrient-poor bunch grasslands to nutrient-rich lawn grasslands. After correction of nutrients translocated to middens by white rhinoceros, lawn grasslands acquire a positive nutrient balance for N (4.3 mg m^{-2} day^{-1}) (but not P [−0.81 mg m^{-2} day^{-1}]), while bunch grasslands remain a negative balance. Thus, mesoherbivores not only respond to heterogeneity in soil and plant nutrients across the landscape but also play a role in maintaining the N enriched status of highly productive and intensively grazed sites (Augustine et al., 2003). Augustine et al. (2003) estimated a N enrichment of 4.38 mg m^{-2} day^{-1} for nutrient-rich areas and a N depletion of 2.46 mg m^{-2} day^{-1}, which is similar to our results (3.5 mg N m^{-2} day^{-1} enrichment vs. 4.8 mg N m^{-2} day^{-1} depletion after correction for export by white rhinoceros). Nevertheless, their effect on the redistribution of nutrients was relatively small compared to what we found for the megagrazer white rhinoceros (7.3 and 9.2 mg N m^{-2} day^{-1} for lawn and bunch grasslands respectively).

Browsers caused a net flow of nutrients from trees/shrubs towards grassland, in agreement with the findings of Sitters et al. (2015). They estimated flows of 0–1.37 mg N m^{-2} day^{-1} and 0–0.07 mg P m^{-2} day^{-1}, which are within the same order of magnitude as our results, although our P flows were smaller (nutrient-poor grassland: 0.015 P m^{-2} day^{-1} and nutrient-rich grassland: 0.005 mg P m^{-2} day^{-1}). These small differences might result from different browser densities, as well as cover of the present vegetation types. Dung deposition by browsers in grasslands tends to decrease with tree density (Sitters et al., 2015).

Interestingly, while the magnitude of our estimated flows of N consumption and return by large herbivores were rather similar, the P returns were about half of what had been consumed. If this mismatch resulted from inaccuracy of our field methods (e.g. missed dung piles), we would expect to find the same gap within our N budgets. Furthermore, we found the same pattern when using the minimum and maximum estimates, suggesting it does not result from the literature estimates used. An alternative explanation is a stoichiometric (N:P ratio) mismatch between large herbivore requirements and their food source. Ecological stoichiometry theory predicts that large herbivores, with their relatively high bone mass and P demand, should recycle more N than P, i.e. consumer-driven nutrient cycling (Sterner, 1990; Sterner & Elser, 2002). If so, they could adjust the N:P ratio of their excreta to resolve this mismatch. Such homeostatic capacity of animals to regulate N:P ratios through their excretion system is similar to nutrient resorption and translocation in plants (Sardans, Rivas-Ubach, & Penuelas, 2012). On average, N:P ratio of excreta used in our study was 16.4, correcting for differences in dung deposition between species. This is relatively high compared to grass N:P ratios, that are generally <10 in South African savanna ecosystems (Ratnam, Sankaran, Hanan, Grant, & Zambatis, 2008; Veldhuis, Hulshof, Fokkema, Berg, & Olff, 2016), suggesting that large herbivores conserve or accumulate relatively more P than N. Not much is known about the N:P requirements of large vertebrate herbivores (Sardans et al., 2012; Sitters et al., 2017). Nevertheless, P has been identified as a key nutrient to

pregnant and lactating ungulates, with an estimated threefold increase at peak of lactation (Murray, 1995). Also, plants have a disproportionate N requirement compared to animals due to the function of this element in photosynthesis (in the enzyme RuBisCo), making plants often more N limited and their consumers more P limited (Sterner & Elser, 2002). These stoichiometric mismatches in combination with retention differences could possibly explain the gap in P budgets found in our study and deserves further investigation.

Dung beetles clearly preferred burying their dung balls in bunch grasslands compared to lawn grassland. Possibly, they prefer relative moist areas with more vegetation cover and loose soil and avoid the dry and compacted grazing lawns (Veldhuis, Howison, Fokkema, Tielens, & Olff, 2014). Generalizing our results to all nutrients deposited showed a relative small, but significant flow from lawn to bunch grassland patches, especially for P. This is not surprising, whereas N is mostly recycled through urine and P through dung (Ruess & McNaughton, 1987). Nevertheless, caution is needed, with this conclusion. Dung beetle activity and community composition has been shown to vary highly between dung piles from different herbivore species (Carpaneto, Mazziotta, & Ieradi, 2010; Finn & Giller, 2002). Furthermore, their activity is highly variable in both space and time (Davis, 1996; Edwards, 1991), which is exemplified by the high variation in amount of dung removed within our experiment. Nevertheless, their potential impact on nutrient cycling is evident (Nichols et al., 2008). Furthermore, in areas or seasons with decreased dung beetles activity, other groups of macrodetritivores, like termites, can also translocate large amounts of herbivore dung (Freymann et al., 2008), aggregating nutrients around their mounds, resulting in nutrient hotspots (Jouquet, Tavernier, Abbadie, & Lepage, 2005). Therefore, further investigation is needed to unravel the overall net effect of macrodetritivores on nutrient redistributions across the landscape.

Within-system nutrient aggregation and translocation by animals generally receive much less attention than other biological processes regarding nutrient cycling in terrestrial ecosystem, such as combustive losses through fires, leaching, N fixation or atmospheric deposition. Nevertheless, comparison with these other important processes that affect ecosystem nutrient budgets, such as fire emissions (1.6–3 mg N m^{-2} day^{-1} and 0.01–0.03 mg P m^{-2} day^{-1} based on fire return intervals of 2–3 years Chen et al., 2010; Laclau, Sama-Poumba, Nzila, Bouillet, & Ranger, 2002; Sitters et al., 2015), biological N fixation (4.5–12 mg N m^{-2} day^{-1} Cleveland et al., 1999; Chen et al., 2010) and N deposition (1.9–2.6 mg N m^{-2} day^{-1} Delon et al., 2012) reveals that especially megagrazers, but also mesoherbivores (and even dung beetles) can make important contributions to local nutrient balances. Within-system nutrient redistributions by animals are approximately of the same order of magnitude as regional atmospheric nutrient in and outputs, making them equally important in understanding ecosystem structure and functioning.

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AUTHORS' CONTRIBUTIONS

M.P.V., H.O. and M.P.B. conceptualized the ideas and designed the study. M.P.V. and M.I.G. collected the data. M.P.V. performed statistical analysis and wrote the first draft of the manuscript. All authors contributed substantially to the revisions.

DATA ACCESSIBILITY

Data and R scripts available from the Dryad Digital Repository https://doi.org/10.5061/dryad.h068r (Veldhuis, Gommers, Olff, & Berg, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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